JOURNAL OF PLANKTON RESEARCH | VOLUME 26 | NUMBER 8 | PAGES 851–857 | 2004

Summer vertical distribution of paralarval gonatid squids in the northeast Pacific

JOHN R. BOWER* AND SHOGO TAKAGI[1]

NORTHERN BIOSPHERE FIELD SCIENCE CENTER, HAKODATE BRANCH, HOKKAIDO UNIVERSITY, JAPAN AND [1]*OSHORO MARU*, FACULTY OF FISHERIES, HOKKAIDO UNIVERSITY, 3-1-1 MINATO-CHO, HAKODATE, HOKKAIDO, 041-8611, JAPAN

*CORRESPONDING AUTHOR: akaika@fish.hokudai.ac.jp

Received August 21, 2002; accepted in principle January 27, 2004; accepted for publication March 24, 2004; published online May 6, 2004

The vertical distribution patterns of paralarvae from several abundant cephalopod taxa were examined from depth-stratified tows in the northeast Pacific (44–56°N, 145–165°W) during three summer surveys in 1999–2001. A total of 309 cephalopods representing 10 taxa in three families were collected. Gonatid squids composed 97% of the total catch, and the most numerous taxa were Berryteuthis anonychus (59% of the total catch), Gonatus spp. (21%) and Gonatopsis borealis (17%). B. anonychus and Gonatus spp. were both most abundant in the upper 20 m; catches of both taxa varied significantly with depth and were significantly higher above the thermocline than in and below the thermocline. Gonatopsis borealis was collected mostly between 20 and 50 m, and catches were significantly higher in the thermocline than above and below the thermocline. Paralarvae of the three major taxa showed no evidence of diel vertical migration. Mantle lengths of Gonatus spp. and G. borealis each varied significantly with depth, and Gonatus spp. showed a strong positive correlation between mantle length and depth.

INTRODUCTION

The most abundant family of cephalopods in the subarctic North Pacific is the Gonatidae. Sixteen species from four genera inhabit the region (Sweeney and Roper, 1998), where they are an important prey for fishes, seabirds and marine mammals, and play a key role in the region's ecosystem (Okutani *et al.*, 1988; Nesis, 1997). Gonatid squids are generally pelagic and occur over a wide depth range; the early life stages occur in near-surface waters, but most species undergo ontogenetic descent to daytime depths below 400 m (Roper and Young, 1975; Nesis, 1997). Some species also undergo extensive diel vertical migrations, ascending at dusk and descending at dawn.

Cephalopod paralarvae are more numerous and easily sampled than the older stages, so paralarval surveys provide one of the best methods for determining gonatid distribution patterns (Okutani *et al.*, 1988), identifying spawning areas (Okutani, 1988), estimating population abundances (Kubodera and Okutani, 1977), and describing life histories (Kubodera, 1982; Falcon *et al.*, 2000). However, before such surveys can be undertaken, the depth distribution of the paralarvae must be determined to design a suitable sampling program. Knowledge of these depth distribution patterns is also needed to determine relations between paralarval concentrations and variables such as seawater temperature and prey availability, and to understand and predict the dispersal of paralarvae by currents.

The vertical distribution patterns of gonatid juveniles and adults in the North Pacific are well studied (Roper and Young, 1975; Nesis, 1989; Nesis and Nikitina, 1995; Hunt and Seibel, 2000), but few studies have examined these patterns in the paralarvae (Okutani, 1966; Kubodera, 1982). In this paper, we present information on the vertical distribution of gonatid paralarvae collected during three summer surveys in the northeast Pacific and examine these patterns in relation to the thermocline. Paralarval size versus depth patterns are also described.

METHOD

Sampling

Samples examined were collected during July 1999, June–July 2000 and June–July 2001 aboard the Hokkaido University ship *Oshoro Maru* in the northeast Pacific.

doi: 10.1093/plankt/fbh081, available online at www.plankt.oupjournals.org

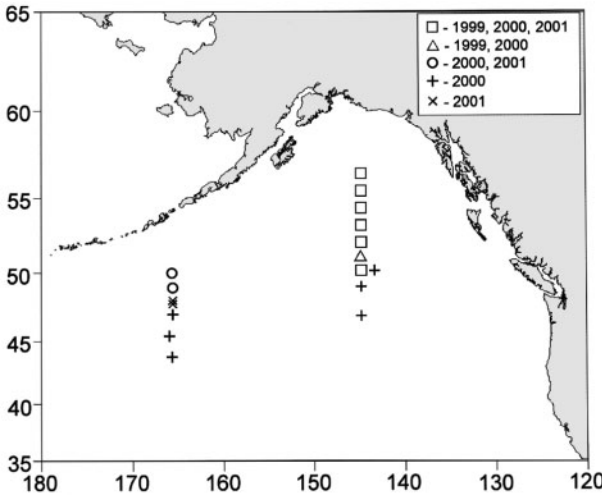

Fig. 1. Locations of sampling sites in the northeast Pacific used to determine the vertical distribution of cephalopod paralarvae.

Sampling stations were located along 145°W between 47° and 56°N, and along 165°W between 44° and 50°N (Figure 1). A total of 37 depth-stratified tows were made with four 0.25 m^2 mouth area Motoda (MTD) horizontal nets (Motoda, 1971) equipped with 333 μm mesh. At each station, the nets were lowered vertically in the water column, towed simultaneously for about 10 min, closed with weighted messengers, and then raised to the surface. Nominal sampling depths were 0, 50, 100 and 200 m in 1999, and 0, 20, 50 and 100 m in 2000 and 2001. Net depths were reached by adjusting the length of wire paid out while maintaining a 45° wire angle. Towing speeds were ~1.5 knots (2.8 km h^{-1}). Retrieved nets were washed, and their contents were preserved in 10% buffered formalin. The volume filtered was estimated using a mechanical flowmeter (Rigosha & Co. Ltd., Tokyo) mounted on each net, and catch abundances were converted to number per 1000 m^3. Paralarvae were identified to the lowest possible taxa using the figures and descriptions in Kubodera and Okutani (Kubodera and Okutani, 1981), and Sweeney *et al.* (Sweeney *et al.*, 1992). The identification of each *Gonatus* sp. specimen was confirmed by dissecting and examining the radular teeth under a compound microsope. The dorsal mantle length (ML) of each paralarva was measured to the nearest 0.1 mm. All sampling in 1999 (7 tows) and 2000 (15 tows) was conducted at night, while sampling in 2001 was conducted during both day (5 tows) and night (10 tows). Time constraints prevented more extensive daytime sampling.

Hydrography

Catches were examined in relation to both sampling depth and the sampling depth's location relative to the thermocline. Seawater temperature data from all stations were taken down to 200 m depth using a Neil Brown MARK IIIB CTD unit to determine the depth range of the thermocline (the highest rate of temperature change) at each station. Each sampling depth was then classified as occurring above, in, or below the thermocline.

Data analysis

Two-factor ANOVA was used to test for differences in catch densities with time and depth. Before analysis, data were tested for homogeneity of variances using Bartlett's test, and, when necessary, the data were transformed. First, data were transformed by $\log(x + 1)$, but when the data remained heterogeneous, the raw data were then transformed by $1/(x + 1)$. If the data remained heterogeneous, a two-way ANOVA was still used [on $\log(x + 1)$ transformed data], but α was set at 0.01 to reduce the risk of Type 1 errors (i.e. incorrectly rejecting a true null hypothesis) (Underwood, 1981). Data from 1999 were excluded from this analysis since the sampling depths differed from those in 2000 and 2001. To examine diel variations in catch densities, collections from the 37 tows were grouped into one of two time periods: day (08:45–17:15 h) and night (21:09–02:24 h). Daytime tows were conducted only in 2001, but catch data from both 2000 and 2001 were used to compare day and night catch densities because the same depths and transects were sampled both years, and catch densities did not differ significantly between the two years (two-factor ANOVA, $P > 0.05$). In addition, a weighted mean depth (WMD) was calculated at each station as $\mathrm{WMD} = \Sigma n_i d_i / \Sigma n_i$, where n_i is the catch density (individuals 1000 m^{-3}) at depth d_i (m), and differences in the WMD between night and day were tested using the Mann–Whitney test. Differences in catch densities from above, in and below the thermocline were tested with the Kruskal–Wallis test, and the nonparametric multiple comparison Dunn test [(Dunn, 1964), also described in (Zar, 1996)] was used when significant differences were observed. Differences in ML with depth were tested with the Kruskal–Wallis test, but to avoid any daytime effect on size distribution (e.g. higher net avoidance by larger individuals during daylight), daytime samples were excluded in this analysis. Level of significance in all tests except for cases of heterogeneous variance noted above was 5%.

RESULTS

Hydrography

The water column was thermally stratified during each survey (Figure 2). The depth of the thermocline occurred

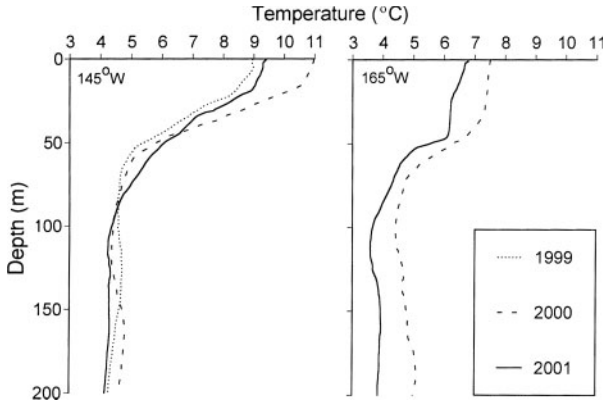

Fig. 2. Vertical temperature profiles along the two sampling transects (145° and 165°W). Data are means of at least four casts along each transect and were collected at 1 m depth intervals.

generally near 20–55 m along 145°W and 40–60 m along 165°W, and varied little along each transect.

Taxonomic composition

A total of 309 cephalopods representing 10 taxa (genera or species) in three families were collected in 84 of the 147 samples (Table I). Gonatid squids composed 97% of the total catch. The most numerous taxa were *Berryteuthis anonychus* (59% of the total catch), *Gonatus* spp. (21%), and *Gonatopsis borealis* (17%). These three taxa were collected in sufficient numbers to allow examination of their vertical abundance and length distribution patterns.

Table I: Summary of all cephalopods collected in the 1999–2001 vertical distribution study

Taxon	Family	Number	Percentage occurrence (n = 147)	ML range (mm)
Berryteuthis anonychus	Gonatidae	181	32.7	2.6–8.6
Gonatopsis borealis	Gonatidae	53	16.3	3.6–8.9
Gonatus spp. undet.	Gonatidae	48	20.4	3.1–10.3
Gonatus sp. type A	Gonatidae	12	6.1	9.3–15.5
Gonatus madokai	Gonatidae	3	1.4	5.5–7.1
Chiroteuthis sp.	Chiroteuthidae	3	2.0	12.4–27.7
Japetella diaphana	Bolitaenidae	2	2.0	7.4–8.6
Gonatus onyx	Gonatidae	1	0.7	19.5
Gonatus pyros	Gonatidae	1	0.7	19.5
Chiroteuthis calyx	Chiroteuthidae	1	0.7	53.0
Unidentified		4	2.7	
All taxa		309	57.1	2.6–53.0

Vertical distribution

Cephalopods were collected at depths between 0 and 100 m, and 96% occurred in the upper 50 m (Figure 3). Catches of all taxa combined (henceforth termed 'overall catches') varied significantly with depth (Table II) and were significantly higher above and in the thermocline than below the thermocline (Table III). Overall catches showed no significant diel differences in catch density (Table II) or weighted mean depth (Table IV).

Berryteuthis anonychus and *Gonatus* spp. were both most abundant near the surface (Figures 3B and C); 92% of *B. anonychus* and 71% of *Gonatus* spp. were collected in the upper 20 m. Catches of both taxa varied significantly with depth (Table II) and were significantly higher above the thermocline than in and below the thermocline (Table III). *Gonatopsis borealis* occurred deeper than *B. anonychus* and *Gonatus* spp.; paralarvae were collected between 20 and 100 m, and 92% occurred between 20 and 50 m (Figure 3D). Catches were significantly higher in the thermocline than above and below the thermocline (Table III). None of the major taxa showed significant

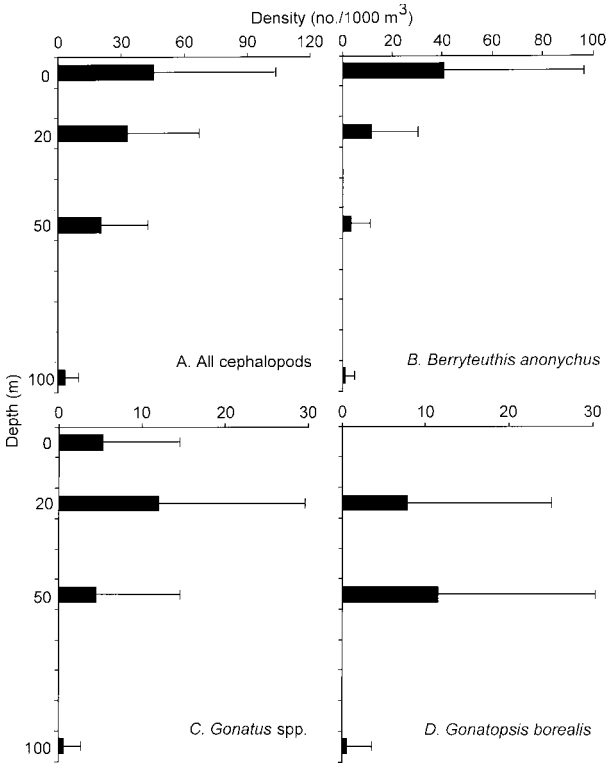

Fig. 3. Vertical distribution of the paralarvae of (**A**) all cephalopods, (**B**) *Berryteuthis anonychus*, (**C**) *Gonatus* spp. and (**D**) *Gonatopsis borealis*. Bars show mean densities (no. per 1000 m^3) at each depth calculated from all samples (1999–2001), and error bars show one standard deviation. Numerals along vertical axis show sampling depths. Sampling was also conducted at 200 m depth in 1999, but no paralarvae were collected. Note variable scale in x-axes.

Table II: Results of two-way ANOVAs testing for differences in density of paralarvae by depth and by time of day in 2000 and 2001

Source of variation	d.f.	Sum of squares	Mean square	*F* ratio	*P* value
All cephalopods					
Time	1	0.44	0.44	0.93	0.34
Depth	3	9.79	3.26	6.83	0.00
Time × depth	3	0.76	0.25	0.53	0.66
Residual	111	53.01	0.48		
Berryteuthis anonychus					
Time	1	0.13	0.13	0.31	0.59
Depth	3	7.41	2.47	6.12	0.00
Time × depth	3	1.00	0.33	0.82	0.48
Residual	111	44.79	0.40		
Gonatus spp.					
Time	1	0.08	0.08	0.28	0.60
Depth	3	4.23	1.41	4.85	0.00
Time × depth	3	0.56	0.19	0.64	0.59
Residual	111	32.29	0.29		
Gonatopsis borealis					
Time	1	0.80	0.80	3.06	0.08
Depth	3	2.52	0.84	3.19	0.03^{NS}
Time × depth	3	0.53	0.18	0.67	0.57
Residual	111	29.20	0.26		

Data from 1999 were excluded from this analysis since the sampling depths differed from those in 2000 and 2001. NS, not significant at $P > 0.01$.

diel differences in catch density (Table II) or weighted mean depth (Table IV). *Gonatus* sp. type A was collected between 20 and 50 m, and *Gonatus madokai* was collected only at 0 m.

Table III: Results of the Kruskal–Wallis testing for differences in catch densities among depth classes and nonparametric multiple comparisons using the Dunn test between the three depth classes: shallow (above the thermocline), thermocline (in the thermocline) and deep (below the thermocline)

	H value	Dunn test
All cephalopods	25.940**	shallow = thermocline > deep
Berryteuthis anonychus	27.403**	shallow > thermocline = deep
Gonatus spp.	8.272*	shallow > thermocline = deep
Gonatopsis borealis	14.150**	thermocline > shallow = deep

H values give the Kruskal–Wallis test statistic. *$P < 0.05$; **$P < 0.01$.

Table IV: Weighted mean depths (m) and standard deviations of the mean depths (in parentheses) for all cephalopods and for the three major taxa in 2000 and 2001

	Day	Night	Overall	*P* value
All cephalopods	14.7 (14.1)	26.0 (14.1)	24.1 (14.5)	0.08
Berryteuthis anonychus	20.0 (24.2)	11.4 (11.2)	13.2 (14.6)	0.60
Gonatus spp.	18.9 (1.9)	24.2 (16.2)	23.4 (15.0)	0.56
Gonatopsis borealis	50.0 (–)	45.0 (20.3)	45.3 (19.7)	0.68

P values give the results of Mann–Whitney testing for diel differences in weighted mean depth.

Length distribution

Mantle lengths of overall catches ranged from 2.6 to 53 mm (median = 4.6 mm), and most (57%) were smaller than 5 mm (Figure 4). Mantle lengths of *Gonatus* spp. and *G. borealis* each varied significantly with depth, and *Gonatus* spp. showed a strong positive correlation between ML and depth (Figure 5). Mantle lengths of *B. anonychus* did not vary significantly with depth.

DISCUSSION

Our results show that during summer in the northeast Pacific, most (96%) cephalopod paralarvae occur in the upper 50 m of the water column. Similar results have been reported in the northwest Pacific, where 91% of paralarvae occur within this depth range (Kubodera, 1982). To date, all studies on the horizontal distribution patterns of paralarval gonatids in the North Pacific have been based on collections made at 0 m depth (Kubodera, 1982; Kubodera and Jefferts, 1984a,b).

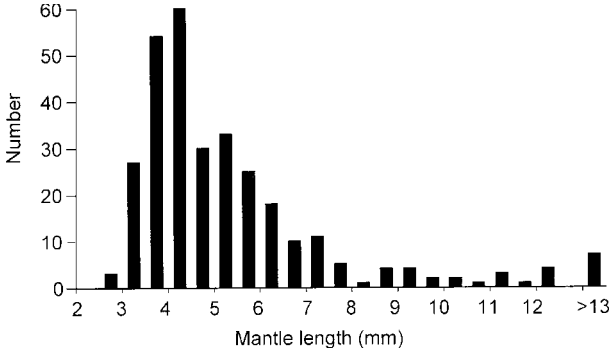

Fig. 4. Length–frequency distribution of all cephalopods collected during the three cruise surveys.

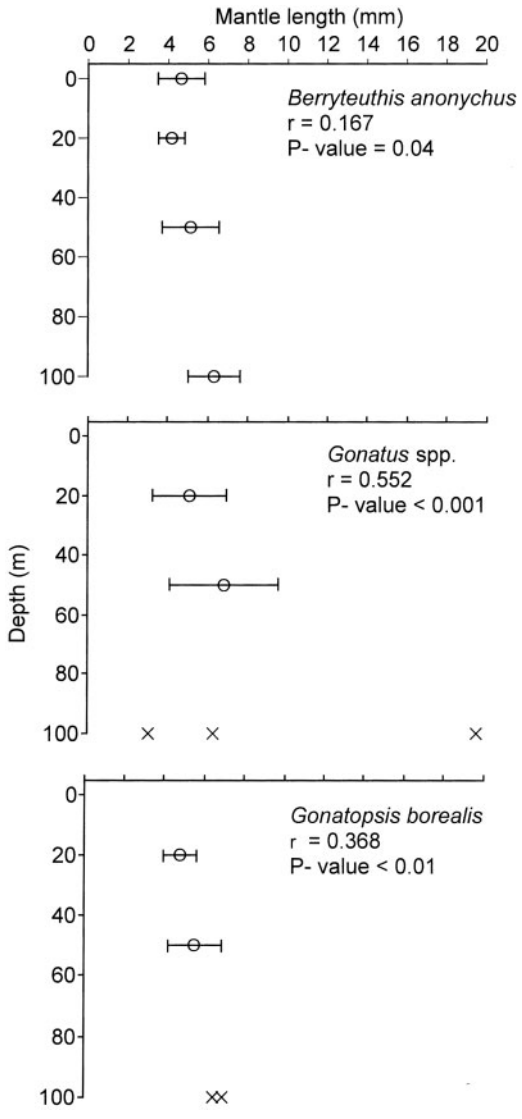

Fig. 5. Nighttime vertical distribution of paralarval mantle lengths of *Berryteuthis anonychus*, *Gonatus* spp. and *Gonatopsis borealis*. Circles show mean length at each depth, and error bars show ± 1 standard deviation. X, actual length measured when fewer than four lengths were available from a particular depth.

To accurately sample this fauna, we suggest that future paralarval surveys sample to at least 50 m.

This study provides further evidence that the vertical distribution patterns of squid paralarvae differ among families (Vecchione, 1987). Overall catches of gonatids, which composed 98% of the total cephalopod catch, were highest near the surface (77% occurred in the upper 20 m). Overall catches of ommastrephids and onychoteuthids off southwest Japan also peak near the surface (Yamamoto and Okutani, 1975), however, those of cranchiids and enoploteuthids in the Arabian Sea and of cranchiids and chiroteuthids off southwest Japan all peak below 30 m (Yamamoto and Okutani, 1975; Piatkowski *et al.*, 1993).

Our results also show that vertical distribution patterns vary among the gonatid taxa; *B. anonychus* and *Gonatus* spp. were most abundant above the thermocline, while *G. borealis* was most abundant within the thermocline. Kubodera (Kubodera, 1982) reported similar findings for gonatid paralarvae in the northwest Pacific, where catches of *Gonatus onyx* and *Gonatus kamtschaticus* peak at 0 m depth, and those of *G. borealis*, *Gonatus* sp. type A and *Berryteuthis magister* peak at 50 m. Other families whose paralarvae show species-specific depth distribution patterns include the Ommastrephidae (Harman and Young, 1985; Saito and Kubodera, 1993) and the Enoploteuthidae (Yamamoto and Okutani, 1975).

The reasons why paralarval gonatids show different vertical profiles are unclear. The general vertical distribution of zooplankton biomass in the world's oceans is food-related, and zooplankton congeners commonly partition vertical space, appearing to avoid competition for similar food resources (Longhurst and Harrison, 1989). However, depth selection is driven by other factors as well as food, including predator avoidance, and environmental limitation by threshold levels of temperature, oxygen, and light (Longhurst and Harrison, 1989; Heath, 1992). None of these factors has been experimentally examined in gonatid paralarvae.

We found no evidence of diel vertical migration in any of the three major taxa, however, more extensive daytime sampling is needed before we can conclusively state that the paralarvae do not undergo diel migration. In vertically migrating gonatids, this behavior appears to develop in post-paralarval stages. *Berryteuthis magister* seems to begin vertical migration at about 50 mm ML (Nesis, 1997). In the Sea of Okhotsk, *G. borealis* begins at about 30 mm ML (Lapko, 1996), while off California, *G. borealis* juveniles as small as 16 mm ML show signs of this behavior (Roper and Young, 1975). The sizes at which vertical migration begins in *Gonatus* spp. (i.e. *G. tinro*, *G. onyx*, *G. californiensis*, *G. pyros* and *G. madokai*) are not clear.

Most gonatids undergo an abrupt ontogenetic descent from the shallow habitat of the young to the deep (generally >400 m) daytime habitat of the adults (Roper and Young, 1975; Nesis, 1997). In *G. borealis*, this descent occurs in maturing or mature adults, while in *Gonatus* spp., it occurs in early juveniles (*G. berryi*, *G. tinro* and *G. onyx*) and late juveniles or subadults (*G. madokai* and *G. kamtschaticus*) (Nesis, 1997). In the present study, both *G. borealis* and *Gonatus* spp. increased in size with increasing depth, suggesting that the paralarvae of these taxa also descend in the water column as they grow. Since all species in these taxa remain in the epipelagic zone

through at least the juvenile stage (Nesis, 1997), this small scale paralarval descent is presumably distinct from the large scale and apparently more abrupt descent to the adult daytime habitat.

Based on the literature and present results, we infer the following possible life cycle scenario for *G. borealis*. Small (4–7 mm ML) paralarvae occur mainly within the thermocline at depths between 20 and 50 m in summer and gradually descend in the water column as they grow. They remain in the epipelagic layer until they reach 16–30 mm ML, at which point they begin diel vertical migration between <400 m at night and 400–700 m during the day (Roper and Young, 1975; Lapko, 1996). This behavior continues through adulthood until the middle or end of maturation, when they are believed to undergo ontogenetic descent before spawning at mesopelagic depths (Nesis and Nikitina, 1995; Nesis, 1997).

Mantle lengths of *B. anonychus* paralarvae did not vary significantly with depth. Larger individuals ranging in size from 10 to 100 mm ML (including mature males) occur at the surface during daylight hours (Bower *et al.*, 2002), indicating that this species does not descend in the water column at sunrise and supporting Nesis's (Nesis, 1997) suggestion that *B. anonychus* may be the only North Pacific gonatid that does not undergo ontogenetic vertical descent.

The present study describes the depth distribution patterns in the Gulf of Alaska during summer, when surface waters are highly stratified. The thermocline in this region forms seasonally at 30–60 m in April or May and persists until September or October (Tully, 1965), when surface waters are again well mixed down to depths of 100–150 m. Since the presence of the thermocline appears to influence the vertical distribution of paralarval gonatids, we expect their depth distribution patterns will differ seasonally.

Gonatid paralarvae are difficult to identify due to poorly understood taxonomy (the paralarval stages from 7 of the 16 known gonatid species in the North Pacific remain undescribed). The lone key published for gonatid paralarvae in the North Pacific (Kubodera and Okutani, 1981) describes the external characteristics of specimens larger than 5 mm ML, however, most (57%) gonatids collected in the present study were smaller than this size. For our specimens smaller than 5 mm ML, we could distinguish *B. anonychus* and *G. borealis* using this key, but not *Gonatus* spp. (genus identification was based on examination of radular teeth). Taxonomic descriptions of *Gonatus* paralarvae smaller than 5 mm ML and of the seven undescribed species are needed before more detailed studies of distribution patterns in the North Pacific can be undertaken.

ACKNOWLEDGEMENTS

We thank Alexander Arkhipkin, Pedro J. Barón, Richard Bower, Tsutomu Ikeda, Tsunemi Kubodera, Kir Nesis, Richard Young and two anonymous reviewers for reviewing the manuscript, and Hiroji Onishi for providing the CTD data. We also thank T. Kubodera for helping identify specimens. This study was supported by grants to both authors from the Japan Society for the Promotion of Science.

REFERENCES

Bower, J. R., Murphy, J. and Sato, Y. (2002) Latitudinal gradients in body size and maturation of *Berryteuthis anonychus* (Cephalopoda: Gonatidae) in the Northeast Pacific. *The Veliger*, **45**, 309–315.

Dunn, O. J. (1964) Multiple comparisons using rank sums. *Technometrics*, **6**, 241–252.

Falcon, L. I., Vecchione, M. and Roper, C. F. E. (2000) Paralarval gonatids (Cephalopoda: Oegopsida) from the Mid-North Atlantic Ocean. *Proc. Biol. Soc. Wash.*, **113**, 532–541.

Harman, R. F. and Young, R. E. (1985) The larvae of ommastrephid squids (Cephalopoda, Teuthoidea) from Hawaiian waters. *Vie Milieu*, **35**, 211–222.

Heath, M. R. (1992) Field investigations of the early life stages of marine fish. *Adv. Mar. Biol.*, **28**, 1–174.

Hunt, J. C. and Seibel, B. A. (2000) Life history of *Gonatus onyx* (Cephalopod: Teuthoidea): ontogenetic changes in habitat, behavior and physiology. *Mar. Biol.*, **136**, 543–552.

Kubodera, T. (1982) Kitataiheiyou akantai kai-iki ni okeru gaiyousei ikarui no seitaigakuteki kenkyuu [Ecological studies of pelagic squids in the subarctic Pacific region]. Hokkaido University, Faculty of Fisheries, Hakodate. 255 pp. Doctoral Dissertation [in Japanese].

Kubodera, T. and Jefferts, K. (1984a) Distribution and abundance of the early life stages of squid, primarily Gonatidae (Cephalopoda, Oegopsida), in the Northern North Pacific (Part 1). *Bull. Natl Sci. Mus. (Japan), A*, **10**, 91–106.

Kubodera, T. and Jefferts, K. (1984b) Distribution and abundance of the early life stages of squid, primarily Gonatidae (Cephalopoda, Oegopsida), in the Northern North Pacific (Part 2). *Bull. Natl Sci. Mus. (Japan), A*, **10**, 165–193.

Kubodera, T. and Okutani, T. (1977) Description of a new species of gonatid squid, *Gonatus madokai*, n. sp., from the northwest Pacific, with notes on morphological changes with growth and distribution in immature stages (Cephalopoda: Oegopsida). *Venus*, **36**, 123–151.

Kubodera, T. and Okutani, T. (1981) The systematics and identification of larval cephalopods from the northern North Pacific. Res. Inst. N. Pac. Fish., Hokkaido Univ. Spe. Vol., pp. 131–159.

Lapko, V. V. (1996) The role of squids in the Sea of Okhotsk communities. *Oceanology*, **35**, 672–677.

Longhurst, A. R. and Harrison, W. G. (1989) The biological pump: profiles of plankton production and consumption in the upper ocean. *Prog. Oceanogr.*, **22**, 47–123.

Motoda, S. (1971) Devices of simple plankton apparatus V. *Bull. Fac. Fish, Hokkaido Univ.*, **22**, 101–106.

Nesis, K. N. (1989) Teuthofauna of the Okhotsk Sea. Biology of squids *Berryteuthis magister* and *Gonatopsis borealis* (Gonatidae). *Zool. Zh.*, **68**, 45–56 [In Russian, with English summary].

Nesis, K. N. (1997) Gonatid squids in the subarctic North Pacific: ecology, biogeography, niche diversity and role in the ecosystem. *Adv. Mar. Biol.*, **32**, 243–324.

Nesis, K. N. and Nikitina, I. V. (1995) Vertical distribution of squids in the southern Okhotsk Sea and northwestern Pacific off Kurile Islands (summer 1992). *Russ. J. Aquat. Ecol.*, **4**, 9–24.

Okutani, T. (1966) Studies on early life history of decapodan Mollusca – II. Planktonic larvae of decapodan cephalopods from the northern North Pacific in summer seasons during 1952–1959. *Bull. Tokai Reg. Fish. Res. Lab.*, **45**, 61–79.

Okutani, T. (1988) Evidence of spawning of *Berryteuthis magister* in the northeastern Pacific (Cephalopoda; Gonatidae). *Bull. Ocean Res. Inst. Univ. Tokyo*, **26**, 193–200.

Okutani, T., Kubodera, T. and Jefferts, K. (1988) Diversity, distribution and ecology of gonatid squids in the subarctic Pacific: a review. *Bull. Ocean Res. Inst. Univ. Tokyo*, **26**, 159–192.

Piatkowski, U., Welsch, W. and Röpke, A. (1993) Distribution of the early life stages of pelagic cephalopods in three geographically different regions of the Arabian Sea. In Okutani, T., O'Dor, R. K. and Kubodera, T. (eds), *Recent Advances in Cephalopod Fisheries Biology*. Tokai University Press, Tokyo, pp. 417–431.

Roper, C. F. E. and Young, R. E. (1975) Vertical distribution of pelagic cephalopods. *Smithson. Contrib. Zool.*, **209**, 1–51.

Saito, H. and Kubodera, T. (1993) Distribution of ommastrephid rhychoteuthion paralarvae (Mollusca, Cephalopoda) in the Kuroshio region. In Okutani, T., O'Dor, R. K. and Kubodera, T. (eds), *Recent Advances in Cephalopod Fisheries Biology*. Tokai University Press, Tokyo, pp. 457–466.

Sweeney, M. J. and Roper, C. F. E. (1998) Classification, type localities, and type repositories of recent Cephalopoda. In Voss, N. A., Vecchione, M., Toll, R. B. and Sweeney, M. J. (eds), Systematics and Biogeography of Cephalopods. *Smithson. Contrib. Zool.*, **586**, 561–599.

Sweeney, M. J., Roper, C. F. E., Mangold, K. M., Clarke, M. R. and Boletzky, S. V. (eds) (1992) 'Larval' and juvenile cephalopods: a manual for their identification. *Smithson. Contrib. Zool.*, **513**, 1–282.

Tully, J. P. (1965) Time series in oceanography. *Trans. R. Soc. Canada*, **3**, 337–366.

Underwood, A. J. (1981) Techniques of analysis of variance in experimental marine biology and ecology. *Oceanog. Mar. Biol. Annu. Rev.*, **19**, 513–605.

Vecchione, M. (1987) Juvenile ecology. In Boyle, P. R. (ed.), *Cephalopod Life Cycles*. Academic Press, London, Vol. **2**, pp. 61–84.

Yamamoto, K. and Okutani, T. (1975) Studies on early life history of decapodan Mollusca – V. Systematics and distribution of epipelagic larvae of decapod cephalopods in the southwestern waters of Japan during the summer in 1970. *Bull. Tokai Reg. Fish. Res. Lab*, **83**, 45–90.

Zar, J. H. (1996) *Biostatistical Analysis*. 3rd ed. Prentice Hall, Upper Saddle River, New Jersey, USA.